

BOTANY.—*Pleuroderris*, a new genus of Middle American ferns.<sup>1</sup>  
WILLIAM R. MAXON, National Museum.

The genus *Hypoderris* R. Br., first mentioned with a few words of description in 1830,<sup>2</sup> was fully described and figured somewhat later by Hooker<sup>3</sup> on the basis of a single species, *H. Brownii* J. Sm., from Trinidad, which has since been found rather commonly in Porto Rico, also in Hispaniola and Grenada, and very recently has been reported from Venezuela.<sup>4</sup> This plant has the general habit and venation of *Tectaria trifoliata*, and in fact closely resembles young individuals of that species. It has been classified nevertheless as belonging not to the Dryopterideae, but to the tribe Woodsieae, because of its curious indusia. These are inferior in attachment and at first subglobose, enclosing the sporangia, but soon become circular, pateriform and flattish, and shallowly lobed on all sides, with fimbriate-ciliate margins.

In addition, five other species have been described under *Hypoderris*, for the most part independently or upon scant material. The latest of these, *H. Stuebelii* Hieron.,<sup>5</sup> founded upon a sterile plant from Ecuador, has since been referred to *Leptochilus*.<sup>6</sup> Of the remaining four, two were described from Nicaragua by Fournier, one from Nicaragua by Prentice, and one from Guatemala by Christ. All five, though exhibiting great variation in leaf form according to age and habitat, as well as in soriation, actually represent but a single species, which departs widely in sorus characters from the genotype, *H. Brownii*, and may be regarded tentatively as constituting a new genus. However, this plant had previously been described from the Darien region as *Lindsaea (Dictyoxiphium) Michleriana* Eaton, which is thus the name-bringing synonym. Because of the laterally attached indusia its repeated description by several authors under *Hypoderris*, in which, as already remarked, the indusium is truly inferior in attachment, is hard to understand, whatever its true relationship may be. Oddly enough the presence of any indusium whatever was overlooked by Baker in describing in the Synopsis Filicum this species once more as new, from Nicaragua, under the name *Polypodium (Dictyopteris) Tatei*. In the same volume also (p. 113) Baker re-

<sup>1</sup> Published by permission of the Secretary of the Smithsonian Institution. Received October 30, 1934.

<sup>2</sup> R. Br. (note) in Wall. Icon. Pl. Asiat. Rar. 1: 16. 1830.

<sup>3</sup> Gen. Fil. pl. 1. 1838.

<sup>4</sup> Revista Sudamer. Bot. 1: 82. 1934.

<sup>5</sup> Hedwigia 46: 323. 1907.

<sup>6</sup> *Leptochilus Stuebelii* (Hieron.) Maxon, Proc. Biol. Soc. Washington 46: 142. 1933.

described *Lindsaea Michleriana* under the genus *Lindsaea*, transferring it however to the subgenus *Diellia*, obviously on the basis of specimens at hand. So we have the rare anomaly of his recognizing one and the same species under three wholly different names, contemporaneously, viz., *Lindsaea Michleriana*, *Hypoderris Seemanni*, and *Polypodium Tatei*!

Type material of all six of the "species" just mentioned has been studied by the writer in connection with a very ample recent series of specimens from the lowland region of Juan Diaz, about 10 miles east of Panama City. From this whole range of specimens the new genus, consisting of a single highly variable species, is described herewith. Its possible origin as a bigeneric hybrid is discussed below. The name adopted relates to the lateral attachment and position of the indusia.

**Pleuroderris** Maxon, gen. nov.

Rhizoma suberectum, paleis castaneis praeditum. Folia multa, stipitibus sulcato-angulatis rufo-castaneis inarticulatis; laminae variabiles anguste deltoideo-oblongae, attenuatae, saepe asymmetricae, basi pinnatisectae vel pinnatae, alibi grosse lobatae; segmenta majora pauca deltoideo-oblonga vel lanceolata, infima semiadnata vel sessilia plerumque repando-crenata vel sinuata, media semiadnata vel adnata, repanda vel sinuata vel subintegra, superiora gradatim minora late conjuncta, laminae apice lato elongato sinuato. Costae subtus elevatae; nervi catadromi distantes obliqui subflexuosi; venatio *Tectariae*, areolis inaequalibus saepe appendiculatis. Sori submarginales vel inter nervos irregulariter et sparse dispositi, dorsales vel compitales, magni, lunati vel vermiformes vel varie curvati, receptaculis plerumque elongatis; indusia lateralia, integra vel interdum ut videtur divisa, obscure ciliolata; sporangia numerosissima longe pedicellata plerumque abortiva vel deformia, annulo incrassato ca. 13-articulato, sporis perpauca alte et tenuiter echinato-alatis; paraphyses nullae.

A terrestrial fern of wet forest ravines, the rhizome stout, suberect, paleaceous. Fronds many, of medium size, ascending, the stipes firm, sulcate-angulate, rufo-castaneous, not jointed to the rhizome; blades variable, narrowly deltoid-oblong, attenuate, often asymmetrical, coarsely lobed, pinnatifid, or (at base) pinnatisect or fully pinnate; pinnae and larger lobes usually few, simple, deltoid-oblong to lance-attenuate, the basal ones of large blades semiadnate or rarely sessile, mostly sinuate to coarsely repand-crenate, those above adnate to semiadnate, long-decurrent, repand to subentire, the upper ones gradually reduced, broadly joined below the broad, greatly elongate, sinuate apex. Costae strongly elevated beneath; veins catadromous, distant, oblique, elevated, subflexuous, nearly reaching the margin; intermediate veinlets freely anastomosing, the costal areoles elongate, nearly or quite connecting the veins at base, the others broadly polygonal, variable, often subdivided, the ultimate areoles with or without simple or forked included veinlets. Sori irregularly disposed in a submarginal zone or sometimes borne in 1 or 2 incomplete sparse rows between the veins, dorsal or compital, mostly large, lunate to irregularly linear or variously curved, the receptacle dark, usually elongate; indusia lateral, entire or (if

greatly elongate) sometimes appearing deeply few-lobed, dark, lustrous, early thrust back and nearly concealed by the sporangia, obscurely ciliolate; sporangia very numerous, long-stalked, mostly abortive or somewhat deformed, the annulus about 13-celled; spores very few, delicately echinate-olate; paraphyses wanting.

TYPE SPECIES: *Lindsaea Michleriana* Eaton, from Colombia, the synonymy being as follows:

**Pleuroderris Michleriana** (Eaton) Maxon

*Lindsaea (Dictyoxiphium) Michleriana* Eaton, Mem. Amer. Acad. n. s. 8: 213. 1860.

*Dictyoxiphium Michlerianum* Moore, Ind. Fil. 319. 1861.

*Hypoderris Seemanni* Prentice, Journ. Bot. Brit. & For. 7: 240. 1869.

*Hypoderris marginalis* Fourn. Bull. Soc. Bot. France 9: 260. 1872.

*Hypoderris adnata* Fourn. Bull. Soc. Bot. France 9: 260. 1872.

*Polypodium (Dictyopteris) Tatei* Baker in Hook. & Baker, Syn. Fil. ed. 2, 506. 1874.

*Hypoderris heteroneuroides* Christ, Bull. Herb. Boiss. II. 6: 292. 1906.

TYPE LOCALITY: "Ad terram prope cataractum Truando Novae Granadae, Schott n. 8."

DISTRIBUTION: Northwestern Colombia to Guatemala, at low elevations.

ILLUSTRATION: Shimek in Bull. Lab. Nat. Hist. Univ. Iowa 4: pl. 18, f. 1-3. 1897; Hook. Icon. Pl. 17: pl. 1670. 1886.

Of the following specimens examined all are in the U. S. National Herbarium (N), unless otherwise indicated:

COLOMBIA: Truando Falls, Intendencia de Chocó, Feb. 1858, Schott 8 (herb. D. C. Eaton; dupl. at N. Y. Bot. Gard.).

PANAMA: Muddy border of small stream near Tapia River, one-half mile south of Pacora road, alt. 30 meters, Nov. 29, 1917, Killip 2706. Deep woods along Pacora River, Dec. 23, 1917, Killip 2734. Deep woods along Tapia River, Dec. 23, 1917, Killip 2746. Deep ravine north of Orange River, along muddy banks of small stream, Jan. 13, 1918, Killip 2787. Ravines of upper Juan Diaz River region, Mar. 10, 1918, Killip 2855. Forest along Juan Diaz River, about 4 miles above Juan Diaz, Jan. 13, 1918, Mrs. L. R. Cornman 648. Wet forest along Tapia River, common, Dec. 1923-Jan. 1924, Standley 26171, 28211. Edge of waterholes and along stream banks, in stiff clay soil often subject to inundation, near Tapia River, June 1-3, 1923, Maxon & Harvey 6666, 6692, 6724.

COSTA RICA: Llanuras de San Carlos, alt. 200 meters, in shade, Apr.-May, 1910, A. & C. Brade 487 (Berlin, N. Y. Bot. Garden; photo. and fragm., N).

NICARAGUA: Chontales, Seemann 206 (Br. Mus.; type of *Hypoderris Seemanni*; photo. and fragm., N). Chontales, in forest, Lévy 501 (type of *H. adnata*, at Paris, not seen; photo. and fragm., N). Chontales, Lévy 501 bis (type of *H. marginalis*, at Paris, not seen; photo. and fragm., N). Chontales, Tate 41/235 (type of *Polypodium Tatei*, at Kew, not seen; dupl. type at Br. Mus.; photo. and fragm. of latter, N). Near Castillo, "found sparingly on the banks of a creek in deep woods," Jan.-Feb., 1893, Shimek s. n. Region of Braggman's Bluff, 1928, Engelsing 269.

GUATEMALA: Cubilquitz, Alta Verapaz, alt. 350 meters, von Tuerckheim (J. D. Smith, no. 8821; type of *H. heteroneuroides*; 3 sheets, N).

Despite this wide array of material, *Pleuroderris Michleriana* is rare in



Fig. 1.—*Pleuroderris Michleriana* (Eaton) Maxon. The type specimen; about two-fifths natural size.

most herbaria, a single exception being the extensive series in the National Herbarium from the Juan Diaz region, Panama. Many of the Panama numbers are represented by two or more sheets, which show not only "abnormal" variations in leaf form but numerous intermediate stages between the young and adult conditions as well. Eaton's type specimen (fig. 1) consists of two fronds that are somewhat immature in leaf form. The well-developed, mature but not extreme form is shown in an incomplete frond of Killip 2787 (fig. 2). Mrs. Cornman's no. 648, from Panama, happens to be an exact match for the type material of *H. Seemanni* and *Polypodium Tatei*, from Nicaragua.

As to relationship, *Pleuroderris* is most like some species of *Tectaria*, but with sori distinctly anomalous in their widely varying structure. The venation is obviously that of *Tectaria*, and the general aspect of the plant hardly less so. The sori arise mostly at the angular intersection of the veinlets which enclose the areoles, as in certain species of *Tectaria*, but they are unique in that the sporangia usually extend in a continuous dorsal line some distance along two or more of the boundary veinlets of an areole and commonly those of an adjacent areole. The sori are thus, as a rule, elongate. Sometimes they are merely lunate or irregularly curved-linear; again they may be T-shaped or Y-shaped, according to the vein-pattern; occasionally they are hippocrepiform or nearly circular in outline. In the last case it will usually be found, on dissection, that the heavy sporangial line runs nearly around the areole and that the laterally attached indusium follows it throughout, being linear in extent though not "linear" in form. Sometimes, also, two or three sori, although of independent origin, arise closely from the same or adjacent areoles and run together at maturity to form a composite "sorus," in which case the indusium may appear coarsely few-lobed. Rarely (e.g., Maxon & Harvey 6692) the sorus is essentially that of *Tectaria*, with roundish-reniform indusium, the sporangia arising from a short receptacle. Besides the types just described, occasionally a sorus is borne also at the expanded tip of an included veinlet.

Details of venation and sori are shown rather imperfectly in the illustrations by Shimek, but this author, in his interesting paper on the ferns of Nicaragua,<sup>7</sup> is apparently the only one to have questioned the reference of the present plant to *Hypoderris*. Although his material was inadequate he contrasted it with the type species, *H. Brownii*, directing special attention to the "transverse" indusium, which is vastly different from the inferior cuplike structure in *H. Brownii*, and concluded that the Nicaraguan plant probably represented a new genus, which however he mistakenly thought should be placed near *Cystopteris*.

The curious position and orientation of the sori in *Pleuroderris* call for comment also. Eaton describes the sori as intramarginal, interrupted, and oblong or linear, and the indusia as slender, interrupted, and "non marginem

<sup>7</sup> Bull. Lab. Nat. Hist. Iowa 4: 115-224. pl. 1-20. 1897.



Fig. 2.—*Pleuroderris Michleriana* (Eaton) Maxon. A well-developed Panama specimen, Killip 2787; about two-fifths natural size.

frondis tegens." Partly because of the submarginal position of the sori in his sparingly fertile specimens he placed the species in *Lindsaea*, subgenus *Dictyoxiphium*, owing to a supposed resemblance of the sori to those of *Dictyoxiphium panamense* Hook., a newly described genotype which Mettenius,<sup>8</sup> knowing the plant only from description and figure, had reduced to *Lindsaea*. However, *Dictyoxiphium* has long since come to be recognized as a valid "monotypic" genus, differing widely in essential morphology from *Lindsaea*. It is a plant having large, simple, sword-shaped fronds similar in venation to *Tectaria*. In spite of similarity in habit and reticulate venation, *Dictyoxiphium panamense* differs markedly from *Pleuroderris* in soriation; the sporangia are borne in an unbroken submarginal line for nearly the entire length of the frond, the sorus being provided with a continuous, delicate, *extrorse* indusium. No such general condition exists in *Pleuroderris*. Here, it is true, the sori are largely borne in a marginal zone, but of those that are actually submarginal a bare majority face outward, some inward, and others in all directions; also they are of all shapes and sizes, and they never form even a subcontinuous series. Moreover, in some fronds the sori are borne far from the margins in a sparse double row between the nerves nearly down to the midrib, as in *Tectaria*; as a rule also the farther they are from the margin the more closely they resemble the sori of that genus. Before the sorus characters were accurately made out, in fact, several early specimens of Mr. Killip's excellent Panama series were referred to *Tectaria*. Further evidence of relationship is afforded by *Tectaria rivalis*,<sup>9</sup> of the Colombia-Panama region, in which the sori are occasionally oblong and provided with a reduced somewhat chitinous indusium strongly suggestive of the kind predominating in *Pleuroderris*.

But if affinity with *Tectaria* may be regarded as established, it appears no less that *Pleuroderris* departs from that genus definitely in the direction of *Dictyoxiphium*, especially in its elongate and occasionally fused sori which tend to occupy a submarginal position. May it not be a hybrid between *Dictyoxiphium panamense* and *Tectaria martinicensis*, even though these belong respectively to the tribes Davallieae and Dryopterideae? Both species were collected in the Juan Diaz region, in very close association with *Pleuroderris*, and both are companion plants of that throughout its range. Additional support for hybridity is found in the highly variable and pronounced asymmetrical shape of many of the blades in *Pleuroderris* and in the sporangia, most of which are somewhat distorted or only partially developed and apparently lack a normal sporogenous content. Coupled with the extreme diversity in shape, position, and size of sori, the last feature is of special importance. Because of the numerous young plants observed in the Juan Diaz region it may be assumed that *Pleuroderris* is there fertile, sparingly so at least, notwithstanding that after repeated examinations only

<sup>8</sup> Fil. Hort. Lips. 105. 1856.

<sup>9</sup> *Aspidium rivale* Mett.; Kuhn, *Linnaea* 36: 120. 1869.

a few mature spores have been found. Though not wholly convincing, the points mentioned, particularly the intermediate character of variable soriation, offer a good deal of ground in support of hybridity.

However, *Tectaria* itself, in the modern sense, embraces plants with widely different sori and is seriously in need of revision as to American material. And in this connection the phylogenetic relationship of several genera should be considered. In particular, *Hypoderris Brownii*, though placed by most authors in the tribe Woodsieae on account of its basal indusia, was regarded by John Smith as allied to the group we now call *Tectaria*. Thus Bower's conclusions,<sup>10</sup> upon morphological grounds, as to the modified characters of *Hypoderris* and certain other genera of the Woodsieae in the direction of the tribe Dryopterideae are of unusual interest.

Similarly *Amphiblestra*, consisting of a single rare Venezuelan species, *A. latifolia* (Humb. & Bonpl.) Presl, although classified by nearly all fern writers as belonging to the tribe Pterideae, was associated by John Smith<sup>11</sup> "with *Dryomenes*, *Dictyopteris*, and *Aspidium*, especially such as *A. macrophyllum*," i.e., *Tectaria*. Kunze<sup>12</sup> figured and redescribed it under *Pteris*, dryly remarking that although in venation it treads upon *Phymatodes*, *Bathmium*, *Dictyoxiphium*, and other genera he was well satisfied to place it in *Pteris*. The habit, simply pinnate blades, and areolate venation are those of a *Tectaria* with very freely appendiculate areoles, but the marginal sori normally are fused to form a continuous longitudinal coenosorus which lacks a true indusium, the slightly recurved but unmodified margin scarcely functioning as such. Nevertheless, Fournier,<sup>13</sup> working with imperfect Nicaraguan material, redescribed the unique *Dictyoxiphium panamense* as a new species of *Amphiblestra*, so strong is the similarity in venation. Bower discusses *Amphiblestra* in connection with progressive anastomosis in *Pteris*, but leaves its systematic position in abeyance. It may indeed be a *Pteris* ally, but equally it may belong near *Tectaria*, in the Dryopterideae. It should be borne in mind that if the existence of similar indusial structures is not necessarily an indication of close relationship among the ferns, such indusia having very probably developed independently and often relatively late in various phyletic lines, so also their absence or even the development of somewhat diverse types of indusia may not always be regarded as weighing heavily against the common evolutionary origin of plants otherwise similar in structure and in habit. *Amphiblestra* is no more puzzling than *Dictyoxiphium*. These and several other groups which in venation and habit resemble *Tectaria* deserve close morphological study. *Pleuroderris* may not be a bigeneric hybrid, as suspected, yet the remarkable intermediates between *Tectaria* and *Hemigramma* which Copeland<sup>14</sup> discusses and illustrates

<sup>10</sup> The Ferns 3: 99-119. 1928.

<sup>11</sup> Hist. Ferns 194. 1875.

<sup>12</sup> Farrnkr. 2: 43-46. pl. 118. 1849.

<sup>13</sup> Bot. Zeit. 31: 8. 1873, as *Amphiblestra simplex*, sp. nov.

<sup>14</sup> Philippine Journ. Sci. Bot. 3: 31. pl. 1-4. 1908.



come to mind as a somewhat similar case. In any event it seems decidedly worth while to place on record such facts as are known about the curious plant here called *Pleuroderris* and to give it temporary status as a genus intermediate between *Tectaria* and *Dictyoxiphium*.

ZOOLOGY.—*The histology of nemie esophagi*. III. *The esophagus of Oesophagostomum dentatum (Rudolphi)*.<sup>1</sup> B. G. CHITWOOD, Bureau of Animal Industry and M. B. CHITWOOD.

This paper is the third of a series dealing with the structure of nemie esophagi. In this paper the same nomenclature is used as in the previous ones (Chitwood and Chitwood, 1934 and 1934). Some notes on the esophagus of *Oesophagostomum dentatum* have been given previously by one of the writers (B. G. Chitwood, 1931), but the detailed structure of this organ was not given.

#### GROSS MORPHOLOGY

The gross morphology of the esophagus of the adult of *Oesophagostomum dentatum* has been given previously by Goodey (1924). The esophagus of this form is in general clavate, terminating posteriorly in an elongate swelling. Regions such as corpus and isthmus are not grossly discernible, but the regions homologous to the corpus and isthmus may be determined on the basis of nuclear distribution. In the specimens studied by the present writers the esophagus was from 360 to 400 $\mu$  long, 150 to 190 $\mu$  of this length comprising the corpus, 50 to 90 $\mu$  the isthmus, 80 to 90 $\mu$  the anterior part of the bulbar region, and 40 to 60 $\mu$  the posterior part of the bulbar region. The internal covering of the esophagus is very definitely modified in the various regions. Throughout the length of the esophagus the walls of the lumen forming the radii converge distally forming an acute angle instead of a cylindrical tube as in oxyurids and rhabditids. At the extreme anterior end the lumen is subtriangular and the walls simple; 10 to 15 $\mu$  posterior to this the lumen becomes much more clearly triradiate, and near the tips of the radii 6 series of thickenings are present, these being attachment points of the radial muscles. These attachment points are continued posteriad to the beginning of the posterior part of the bulbar region. In the anterior region of the corpus, minute spines project internally from the wall of the esophagus. The dorsal esophageal gland opens at the anterior end of the corpus, but the position of the orifices of the subventral glands has not been determined with certainty by the writers. Goodey (1924) stated that their orifices were situated just anterior to the beginning of the bulbar region.

The esophagus of this species, like the esophagi of other members of the Strongyloidea, undergoes many changes during development. In the first-stage larva it consists of a corpus, isthmus, and valvulate bulb identical in

<sup>1</sup> Received October 18, 1934.